

ART. XXIII.—*The Syrinx of the Common Fowl, its Structure and Development.*

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(With Plates XVIII.-XXIV.).

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Introduction.

The material for this investigation consisted of a large number of syringes of the adult common fowl, and of sets of longitudinal and transverse serial sections of chick embryos, in all stages, from nine days' incubation until the time of hatching, examined in regard to the structure and development of the syrinx; and lastly, embryos at several stages were dissected, especially in regard to the relation of the respiratory air sacs to the syrinx.

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Adult Structure.

As far as the adult structure is concerned, the description which follows corroborates the work of, and gives details additional to those given by Wunderlich (1884, p. 79), who has figured the adult syrinx, and Garrod (1879, p. 377), who, in discussing the conformation of the thoracic extremity of the trachea in birds, deals briefly with the condition in *Gallus bankiva*.

I.—*External Aspect.*

The syrinx or vocal organ of the bird (known previously to Huxley as the lower larynx), is constituted by the modified tracheo-bronchial junction, and in the common fowl both trachea and bronchi are involved in its formation. Each side of the lower tracheal extremity presents a membranous appearance. The ventral surface is mainly occupied by a triangular-shaped plate, more or less cartilaginous in structure; and a similar but smaller plate is present on the dorsal surface. The chamber of the syrinx or "tympanum," is seen to be compressed from side to side, but there is a corresponding increase of depth dorso-ventrally. The outer walls of the bronchi are strengthened by semi-rings of cartilage, while the inner walls are membranous, and bands of fibrous tissue termed the bronchidesmus, pass from one bronchus to the other, so as to enclose beneath the bronchial junction a large air space. The body of the ventral triangular plate is seen to be continuous with that of the dorsal surface, through the medium of a semi-cartilaginous or calcareous rod, termed the pessulus. The basal angles of the plates articulate with the extremities of the first bronchial semi-rings, and in close relation to each side of the plates are the lower tracheal rings, which are much modified, lying embedded in the thin membranous walls of the trachea. As to the syringeal muscles, they do not appear to be directly and intimately associated with the syringeal membranes, as they are in many other birds. Lastly, the whole of this syringeal chamber, or "tympanum," is in close relation to respiratory air sacs, which extend, not only up between the two bronchi, but also around each surface of the syrinx, so that the whole organ is completely enveloped.

II.—*Detailed structure of the syrinx.*

The syrinx consists of the following structures:—

1. Supporting framework,
2. Syringeal membranes,
3. Syringeal muscles,
4. Syringeal air sacs.

1. Supporting framework.

In place of the simple cartilaginous tracheal rings and bronchial semi-rings, there has been much modification at the tracheo-bronchial junction, in the formation of the supporting framework of the syrinx, so that we may distinguish the following elements:—

- (a) The rod-like portion of the pessulus.
- (b) Dorsal triangular plate of the pessulus.
- (c) Ventral triangular plate of the pessulus.
- (d) Last six tracheal rings.
- (e) First two bronchial semi-rings.

(a) Pessulus.—The pessulus is situated just below the junction of the bronchi, and it passes from the ventral to the dorsal surface of the tracheal extremity. It is rod-like in shape, and in the adult partly osseous in structure. Ventrally, it expands into the body of a large median triangular plate, with a cranially-directed apex. Dorsally, it is continued into a similar but smaller plate, the whole structure (rod and two plates) resembling somewhat a double-headed bolt. Along the cranial margin of the pessulus there is a thin fold of mucous membrane, termed the *membrana semilunaris*.

(b) Ventral Triangular Plate.—As already stated, this is situated on the ventral surface of the tracheal extremity. Its apex extends as far cranially as to lie just behind the fourth last tracheal ring. Its basal angles articulate with the extremities of the first bronchial semi-rings. Its lateral edges are in close relation to the last three tracheal rings, fusion taking place usually only with the last ring. Its body is partly calcareous, and may be even osseous in structure.

(c) Dorsal triangular plate.—It is situated on the dorsal surface of the tracheal extremity, and its apex extends cranially between the dorsal ends of the last two tracheal rings, but does not quite reach the ante-penultimate ring. The dorsal ends of the first bronchial semi-rings articulate with the lateral angles of the plate, and with its sides the ends of the last two tracheal rings are in close relation, but do not fuse.

(d) Last six tracheal rings.—(i.) Last tracheal ring. Of the six rings, this is the most developed. It is not flattened, but rounded. Ventrally, it widens considerably, and fuses with the triangular plate, but dorsally, it presses closely against the plate, without fusing.

(ii.) Penultimate ring. This second-last ring is band-like, and rather wider than the others. Its ventral extremities press closely against the sides of the ventral triangular plate, while dorsally the ends lie on each side of the dorsal plate.

(iii.) Ante-penultimate ring. The third-last ring is more reduced. It is made up of two straight, lateral, band-like rudiments. Its ventral ends do not fuse, but lie on each side, against the apex of the ventral triangular plate. Its dorsal ends taper considerably, and come to lie close to each other, without fusing, and just beyond the apex of the dorsal triangular plate.

(iv.) Fourth-last ring. This ring is so reduced and incomplete as to be represented by a mere thread-like band, situated a little beyond the apex of the ventral triangular plate. The left side is thinner, and does not go much further than half-way towards the dorsal surface, but generally fuses with the third-last ring. The right side is wider, and nearly reaches to the dorsal surface. Ventrally, the ends come very close together.

(v.) Fifth-last ring. This ring differs from a normal ring in being slightly incomplete dorsally, where its ends are turned downwards, towards the apex of the triangular plate. It is flattened, and purely cartilaginous in structure.

(vi.) Sixth-last ring. This is the only complete ring of the syrinx, and differs from those above the rings of the syrinx in not being osseous in structure.

(e) Bronchial semi-rings.—The first two semi-rings only are especially modified in connection with the syrinx. The first is characterised by its large size, thickness and marked curvature, the concavity being directed cranially. It is not flattened, but round, and it articulates very intimately with the basal angles of both ventral and dorsal triangular plates.

The second semi-ring has its ventral ends fused with those of the first, but dorsally they are widely separated.

2. Syringeal membranes.—As already stated, the syrinx has a general membranous appearance, and on closer examination several distinct membranes may be recognised. As a whole, they are characterised by being set or stretched between an air space on either side. As will be seen, the wall of each membrane has histologically three layers. The following membranes may be distinguished :—

- (a) Membranæ externæ,
- (b) Membranæ internæ,
- (c) Membranæ tracheales,
- (d) Membrana semilunaris,
- (e) Bronchidesmus.

(a) Membranæ externæ.—These membranes are situated one on each side of the tracheal lower extremity. They are very thin

and translucent, and occupy the region between the last tracheal ring and the first bronchial semi-ring. External to it is a respiratory air sac, internal to it is the air space of the trachea, and so the membrane is stretched between two air chambers. The wall of the membrane is three-layered. The middle layer is of mesoblastic origin, the other two being of hypoblastic origin.

(b) *Membranæ internæ*.—These membranes are the thin inner walls of the bronchi, and thus occupy the region between the free ends of the bronchial semi-rings. Above they are limited by the pessulus, and below, to some extent, by the bronchidesmus. The space between the two membranes is occupied by the subpessular air space. As before, the membrane has three layers, the innermost being bronchial epithelium, much folded in one part, the middle layer of mesoblastic origin, and the outer the epithelium of the air sac.

(c) *Bronchidesmus*.—This is a fibrous band, passing between the two *membranæ internæ*. It is set somewhat obliquely, and is formed by the apposition of the unsymmetrical right and left interbronchial respiratory air sacs.

(d) *Membranæ tracheales*.—These are the membranous lateral walls of the tracheal extremity. Embedded in them lie the last five tracheal rings, which are so flattened and reduced that, notwithstanding this cartilaginous framework, the walls are thin, translucent and membranous. They are separated caudally from the *membranæ externæ* by the last tracheal ring. Like these latter membranes, they are composed of three layers, and set between the air in the trachea and that in the respiratory air sacs.

(e) *Membrana semilunaris*.—This is a thin fold of mucous membrane, overlying and projecting from the cranial border of the pessulus. It consists histologically of an inner core of mesoblastic origin, overlaid on each side by the tracheal epithelium. It is only slightly marked in the adult, but is of considerable size at one stage in the embryo.

3. *Muscles*.—In addition to the sterno-tracheales and tracheo-clavicular muscles, which have relation both to the lower and upper parts of the trachea, there are also present a dorsal and a ventral pair of muscles. These latter two pairs correspond to the true syringeal muscles of other birds, in which, however, they may be of considerable size, and more intimately associated with the syrinx. These true syringeal muscles are said to be derived from the sterno-hyoid group of muscles, and pass down the trachea to the syrinx (see *Syrinx Dictionary of Birds*, by Newton), but in the common

fowl they reach only as far as the eleventh or twelfth last tracheal ring, while the syrinx does not begin until the sixth-last ring. Thus these muscles of the common fowl have no very close relation to the membranes of the syrinx.

4. *Respiratory Air Sacs.*—The air sacs completely surround the syrinx. This envelope is not a simple one, but a composite one, in which the several air sacs are in intimate contact with each other, and with the syringeal membranes. In development, they are seen to be derived from the third entobronchus of the lung. The third entobronchus terminates in a stem, which subdivides into two main stems, of which one, opening into the interclavicular sac, goes to form the syringeal air sacs, while the other opens out into the anterior thoracic air sac. As the stem of the interclavicular or syringeal air sacs ascends from the third entobronchus of the lung to the interbronchial region, it expands into several air sacs, which take up different positions in relation to the parts of the syrinx.

A large ventral sac passes over the ventro-cranial region of the bronchus and triangular plate, and comes to occupy the ventro-lateral region of the syrinx.

A large sac from the right side extends up so far as to lie close beneath the pessulus, the sub-pessular air sac. On each side it is in relation to the membranæ internæ.

Another large sac passes dorsally from between the bronchi, and then opens out into dorso-lateral sacs. The most cranial one is large, and comes to occupy the dorso-lateral region of the syrinx.

Other branches pass off, and become related to structures apart from the syrinx, one main branch and several smaller ones returning to the lung tissue, and so constituting the recurrent branches of the interclavicular sac. The recent research of Juillet, 1912 (Chap. IV.), showing that the direct stem of the interclavicular sac arises in common with the stem of the anterior thoracic sac, is here confirmed. What was formerly thought to be the direct bronchial stem, he has shown to be the indirect recurrent interclavicular branch. Thus the stem of the interclavicular sac, besides giving off its recurrent branches, expands into the interclavicular region, where it gives rise to the syringeal air sacs.

Embryonic Development.

Passing now to the embryonic condition of the organ, a general survey of its development will first be given, followed by a detailed description of the gradual appearance, in time, of the several parts of the syrinx.

III.—*General Survey.*

Concurrent with the development of the trachea and bronchi as hypoblastic outgrowths, the surrounding primitive mesoblast begins to gradually condense, or concentrate, around them, and as early as the end of the third day of incubation this concentration is clearly indicated. As development proceeds, there are formed at regular intervals in this denser mesoblast, concentrations of tissue, each gradually assuming a ring-like form.

Ultimately, by differentiation, they give rise to the more or less cartilaginous framework of the trachea and bronchi. However, in the region of the tracheo-bronchial junction, these ring-like concentrations are considerably specialised, to form the supporting structure of the syrinx. The most distinctive modification, and one whose bolt-like form is so characteristic of the common fowl is the appearance of a rod-like concentration just between the conjoining bronchi, which expands into a dorsal and a ventral plate, and hence, from its shape, has been well called the pessulus. As the ring-like concentrations of the syrinx assume definition, there is a gradual change in regard to their relative size, some becoming strongly, others poorly, developed, even to the extent of becoming mere vestiges. There is also a change in shape, some losing their circular form, and becoming flatter and flatter, until merely band-like rudiments. Still further, there is modification not only in degree of development, but also in their mutual relations and relation to the dorsal and ventral pessular plates.

As the supporting framework thus develops, the membranes gradually appear, and become more and more differentiated from the surrounding tissue. The first to be indicated are the membranæ externæ, and, from the time when the tracheo-bronchial framework begins to appear, the position of these membranes is recognised by the greater interval between the last tracheal ring and the first bronchial semi-ring. In this interval the wall of the trachea gradually becomes deflected towards and into the lumen, while the tissue subsequently changes in structure, and finally gives rise to the very thin oval-shaped membrane of the adult. The next membrane to appear is the membrana semilunaris, which becomes thrown up as a wedge-shaped fold, capping the cranial border of the pessulus. It increases considerably in size, but in the adult it has become relatively small. Along with the development of this fold, the inner walls of the bronchi begin to be clearly separated from each other by a space, so as to give rise to the membranæ internæ. This

is accomplished by the upgrowth of the interclavicular sacs from the lung into the interbronchial region. The stem of the interclavicular sac and that of the anterior thoracic air sacs, are the bifureations of the main stem of the third entobronchus of the lung. The interbronchial sacs are not symmetrical, the large sub-pessular sac being derived from the right side, and in contact with both membranæ internæ. As a result, there is a three-layered band of tissue gradually developed, separating the air-spaces of the right and left sides, and tending to connect obliquely the two membranes. This band of tissue becomes the bronchidesmus, which, in the adult, is tough and fibrous. The membranæ tracheales, or the two lateral walls of the upper part of the syrinx, have the last five or six tracheal rings embedded in their tissue, and even up to the time of hatching, these walls remain thick. After hatching, however, when the embedded rings rapidly begin to flatten, the walls become distinctly membranous and tough, and finally constitute in the adult the membranæ tracheales.

It has already been mentioned what an intimate relationship comes to exist between the membranæ internæ and interbronchial air sacs. A similar relationship comes about in regard to the membranæ externæ and tracheales. The stem of the interclavicular sac not only gives off the interbronchial and subpessular sacs, but also gives off large ventro-lateral and dorso-lateral sacs. The ventral sac expands over the bronchi and the triangular plate into a large sac, which gradually becomes closely applied to the ventro-lateral half of the membranæ externæ and tracheales. The dorsal sac expands around the dorsal surface of the bronchus and triangular plate, giving off several dilatations, one large one coming to occupy the dorso-lateral half of the membranæ externæ and tracheales.

Thus the whole syrinx becomes enveloped in air sacs, and this fact, together with the poor development of the syringeal muscles, is suggestive of the cause of vibration of the syringeal membranes. (Pls. XVIII. and XIX., figs. 1, 2, 3.)

The syringeal muscles make their appearance at about the end of the second week of incubation, where they are seen developing beneath the tracheo-clavicular muscles. A dorsal and a ventral pair develop, but they do not extend down as far as the syrinx, stopping short at about the eleventh or twelfth tracheal ring from the caudal end.

Such is the general survey of the developing organ. A more detailed description of various stages will now be given, showing the development of the several parts, in order of time.

IV.—*Developing Elements at Different Stages.*

1. Nine days' incubation.—After nine days of incubation, a concentration begins to take place in the enveloping dense mesoblast, and this is the first indication of what will be the first bronchial semi-ring.

2. Ten days.—Early in the stage there has also appeared the first indication of the last tracheal ring, but it is not so definitely marked as the first bronchial has now become. Just between the uniting bronchi, the mesoblast tissue is becoming very concentrated, and from this the pessulus will develop later. Towards the close of the tenth day, the penultimate ring and the second bronchial semi-ring are just forming, while the first bronchial semi-ring and the last tracheal ring are now more clearly differentiated from the surrounding tissue. Between these latter two there is a considerable interval, and in each case they cause the hypoblastic epithelium to project somewhat into the lumen, the interval marking the site of the future membrana externa.

3. Eleven and twelve days.—In an early stage of an eleven days' embryo, the pessulus begins to be indicated, as a change gradually takes place in the centre of the dense interbronchial mesoblast. Also, the developing tracheo-bronchial rings are becoming more differentiated, and a little later in the eleventh day, and by the twelfth day, the ante-penultimate fourth and fifth-last rings have just appeared, but are more marked in the dorsal region. Also, cranial to these, a large number of tracheal rings are developing, while caudally the third bronchial semi-ring has appeared, and the fourth is just beginning. The pessular mesoblast, in which the pessulus is developing, now extends to both dorsal and ventral surfaces of the tracheal extremity, where it is expanded to form dorsal and ventral plates of dense mesoblast, from which the triangular cartilaginous plates will arise. (Pl. XIX., fig. 4.) At this stage, thus, the main elements of the supporting framework are all indicated, but while the first bronchial semi-ring and the last tracheal ring are now large and clearly marked, the remainder are small, less definite, and imperfect. The degree of development is seen by comparing the extent to which each element has passed beyond the mid-lateral region, towards the dorsal and ventral surfaces. The last tracheal and first bronchial reach the dorsal and ventral surfaces, where there is fusion with the pessular plates of dense mesoblast, except in the case of the ventral ends of the first bronchial, which lie free just caudal to the plate of mesoblast. This ventral plate

also receives the ventral ends of the second and third-last rings, while just beyond them are the ventral ends of the fourth, fifth and sixth-last rings. Those of the fourth and fifth fuse on each side, and then with those of the other side, while those of the sixth fuse in the mid-line, and lie quite separate from the others. As to the extent of dorsal development, the fourth and fifth-last scarcely pass the mid-lateral line before fading away, and then, likewise, a little further, the third and the sixth-last. Still further dorsally, the second-last fades away, as well as the remnants of the bronchial semi-rings, except the first, which, together with the last tracheal ring, passes right to the dorsal surface, there merging into the pessular mesoblast plate. Even at this early stage, it is noticeable that the ventral development is much less restricted than that of the dorsal.

4. Thirteen days.—By this stage a considerable number of bronchial semi-rings and tracheal rings, not directly concerned with the syrinx, have begun to form. Those concerned with the syrinx have all become more distinctive, especially the last two tracheal rings, and the first two bronchial semi-rings. This is seen in regard to their structure, size and outline. The interval between the last tracheal and first bronchial is greater, and hence the rudiments of the *membranae externae* are more marked. The difference in size is even now very noticeable, the third, fourth and fifth last being relatively very small. The more distinctive structure and outline is seen, not only in the rings, but also in the pessulus and its plates, concentric circles of cells are now seen surrounding the pessulus. As to the greater extent of development, compared with the last stage, this is seen in a few particulars. In the dorsal region, the extremities of the last tracheal ring and the first bronchial semi-ring are now being clearly differentiated from the dense dorsal mesoblast, so that their ends lie somewhat free. (Pl. XX., fig. 9.)

As early as this stage a variation is at times apparent. The fourth-last ring, which is most poorly developed, and passes little towards the dorsal surface, usually fuses on the left side with the third last, but sometimes, though less often, the fusion takes place with the fifth ring. This fusion on the left side is indicated at this stage, while on the right the ends are quite free. As in the last stage, there is little dorso-lateral development of this ring. As for the second, fifth and sixth-last rings, they now reach the dorsal surface where they merge into the dorsal plate of mesoblast, from which the dorsal triangular plate is not yet clearly defined. The chief changes in the ventral region are the separation of the fifth ring

from the fourth ring, so that it becomes like the sixth ring. The fourth ring is still associated with the apex of the dense ventral plate, which is becoming definitely triangular in shape. (Pl. XIX., fig. 5.)

At a little later stage, on the thirteenth day, more changes are apparent. The whole framework is of greater size, and more definite outline, and rapidly approaching the cartilaginous stage. The boundaries of the pessulus are now well defined. Ventrally, the framework now presents its characteristic configuration—namely, the last four tracheal rings are clearly involved in fusion with the sides and apex of the ventral triangular plate, while its basal angles articulate with the ends of the first bronchial semi-rings, and with the latter the ends of the second bronchial have begun to fuse. (Pl. XIX., fig. 5.)

Dorsally, the ends of the ante-penultimate have now extended to the dorsal dense mesoblast.

5. Fourteen days.—As before, there is increased size and differentiation in the supporting framework, while other developments have appeared. On each side of the dorsal triangular plate lie the free ends of the last tracheal, penultimate and first bronchial. Just beyond the apex of the plate, there are the ends of the ante-penultimate, which are now clearly defined and pressed against each other and the apex of the plate, yet without fusing. The dorsal ends of the fifth-last similarly come close together in the middle line, without fusing, but those of the sixth last do fuse, so that this ring becomes the only complete one associated with the syrinx. The fourth-last is still small, and now passes further dorsal than before. Ventrally, no marked change has resulted. In addition to these changes in the supporting framework, two other changes are apparent. Firstly, the medial hypoblastic walls of the bronchi are thrown into folds; and, secondly, the syringeal air sacs can now be seen pushing their way up from the third entobronchus of the lung towards the interbronchial tissue. (Pl. XVII., fig. 1; and Pl. XXIV., figs. 19 and 24.)

As yet the membranæ internæ are not formed. The stem of the interclavicular or syringeal air sacs has, however, divided into its three main diverticula—namely, the large ventral sac, the dorsal sac, and the smaller cranially-directed one, which, from the right side, will become the sub-pessular sac. (Pl. XXIV., fig. 19.)

This latter change subsequently becomes of great importance in its bearing on the whole syrinx, and this fact becomes more and more evident in following stages.

6. Fifteen days.—This stage of development is of considerable importance, since, by this time, the foundation of all the main structures of the syrinx has been laid. (Pl. XVIII., fig. 27.)

The supporting framework, with all its elements, is definitely formed, all the syringeal membranes are to some extent indicated, the syringeal muscles are developing, and lastly, the syringeal air sacs begin to show intimate relationship with the syrinx as a whole. As to the general enveloping mesoblastic tissue, it is now losing its dense character, and gradually changing into a reticular meshwork, but the tissue closely around the lower tracheal rings is still dense, and is made up of several layers of flattened cells.

Supporting framework.—A few changes have taken place. Previous to this stage, the last four tracheal rings have been fused with the sides and apex of the ventral triangular plate; but now, at this stage, there is the beginning of a change, which later results in the separation of all but the last ring from the plate. (Pls. XIX., XX., figs. 4 and 8.)

This goes on gradually, and reaches completion some time after the hatched condition. There is variation in the actual time of separation, but at the end of the fifteenth day the apex of the ventral plate is no longer intimately fused with the fourth-last ring. Again, the ends of the third-last now articulate with each side of the apex, so that only the last two rings remain fused with the sides of the plate. (Pl. XIX., fig. 6.)

It may also be noticed that the ventral ends of the first two bronchial semi-rings are now more definitely fused. The smaller size of the dorsal triangular plate, as compared with the ventral one, is now seen. Also, it is not directly fused with any of the tracheo-bronchial rings. As before, its lateral angles articulate with the first bronchial semi-ring, its sides with the ends of the last two tracheal rings, and its apex articulates with the ante-penultimate ring, whose ends are now fusing.

On the left side, the fourth-last ring fuses at its extremity with the fifth-last ring, just before the extremities come close together in the mid-line.

Syringeal membranes. (Pl. XVIII., fig. 2.)—At the close of the fifteenth day, the membrana semilunaris first begins to appear, capping the more ventral region of the pessular rod. It is wedge-shaped, and simply consists of a mesoblastic interior, covered by the hypoblastic epithelium. The unattached edge projects slightly into the lumen of the tracheal extremity. The membranæ externæ be-

tween the tracheal rings and the bronchial semi-rings are now larger in size, and somewhat deflected into the lumen of the syrinx. Their walls are still thick and dense in structure.

The *membranæ internæ* are now developing from the inner walls of the bronchi, between the free end of the bronchial semi-rings. At first, the mesoblastic tissue between the bronchi is one continuous sheet, but at the close of the fifteenth day the inter-bronchial air sacs have so extended upwards as to reach almost to the pessulus; hence the mesoblastic tissue is divided into two layers. In this way the *membranæ internæ* first begin to form. Their walls have three layers, and the mesoblastic layer is as yet of considerable thickness. As yet the right air sac has not completed the splitting of the mesoblast in the dorsal region, where the two membranes have not become differentiated. The hypoblastic epithelium of the membranes is thickened, and contains spaces, so that it tends to become folded. With the pushing up of the two inter-bronchial air sacs, the bronchidesmus becomes formed at this stage. It consists of the two thin walls of the right and left air sacs, with a strand of mesoblastic tissue between them, and continuous with the mesoblastic walls of the *membranæ internæ*. The intimate association of these three layers constitutes the bronchidesmus, and, owing to the greater and asymmetrical development of the right sac, the membrane is directed obliquely between the bronchi.

The *membranæ tracheales* do not become membranous in structure until after hatching, and hence at this stage their walls are thick, and the tracheal rings embedded in them have only just begun to flatten. There is also to be seen a denser tissue, connecting the rings.

Muscles of the syrinx (Pl. XVIII., fig. 2).—By this stage, the sterno-tracheales and tracheo-clavicular muscles are well marked, lying close to the ventral and lateral sides of the trachea. The tracheo-clavicular leave the latter walls of the trachea just above the region of the eleventh and twelfth-last tracheal rings. Between these muscles and the trachea the syringeal muscles are developing and extending down a short distance towards the syrinx. They do not reach the syrinx, and, as yet, they are not clearly differentiated into a dorsal and a ventral pair.

Syringeal air sacs.—The syringeal air sacs have now become much expanded, both between the bronchi, and also to the lateral side of the syrinx. On the right side the sub-pessular air sac has been given off, and thus the *membranæ internæ* are now defined, except

in the more dorsal region. On the left side the dorsal dilatation passes around the bronchus, and is approaching the *membrana externa*; other air spaces are also present, coming towards the lateral walls of the syrxinx. (Pl. XVIII., fig. 2.)

7. Sixteen days.—The chief progressive changes that have taken place at the close of the sixteenth day have to do with the expansion of the syringeal air sacs. (Pls. XXI., XXII., and XXIII., figs. 11-16.) Very little change has occurred in the supporting framework. The ventral triangular plate has, fused to its sides, only the extremities of the last tracheal ring, and one end of the penultimate, the other end, usually the right one, having separated off from the plate. (Pl. XX., fig. 7.) The apex of the dorsal plate has become more acute, and is surrounded, as before, by the free ends of the third, fourth and fifth-last rings, the ends of the fifth ring now tending to turn downwards, towards the apex of the plate. Much variation and irregularity is at times seen at this stage, and in later stages, in regard to the fused or unfused condition of the dorsal end of the above rings. The ends of the fifth-last may, or may not, be fused. The different rings may be free from each other, or partially fused, the tendency being, however, towards fusion of these three rings in this dorsal region. In one case the fifth ring was fused on one side with that of the sixth.

As to the membranes, owing to the growth of the air sacs, they all now take on their characteristic structure of three layers, and are set between an air cavity on either side of them; so that eventually, in the adult, this probably becomes a condition of their vibration during the alternate expansion and contraction of these air spaces, as the air goes in and out. The *membrana semilunaris* is now very well marked, and extends along the whole cranial border of the *pessulus*. The tissue of the *membranæ externæ* is more reticular, and their walls become thinner as the air sacs push into them. (Pl. XXIII., fig. 15.) The *membranæ internæ* are now completely formed. Their walls are thinner, owing to the reduction of the mesoblastic tissue. To about the middle of the left membrane the *bronchidesmus* is attached. Little change has taken place in the *membranæ tracheales*, except that its tissue has become more reticular, the middle rings smaller, and the membrane as a whole thinner.

Syringeal air sacs.—As this is the stage at which the air sacs take up their characteristic relation to the membranes, their origin, extent and position will now be somewhat fully described. (Pls. XXI., XXII., and XXIII., figs. 11-16.)

The mesobronchus of the lung, while passing from the medial to the lateral region of the lung, gives off its third entobronchus. (Pls. XXIII. and XXIV., figs. 17, 18, 22.) The third entobronchus is directed medially and ventrally, and subdivides into three main branches. Almost immediately it gives off its first branch, which is directed caudally, medially, and slightly dorsally, and is confined to the lung itself. (Pl. XXIV., figs. 18, 22.) The stem then passes ventrally, and in the ventro-medial region of the lung, bifurcates, the slightly smaller branch is the stem of the interclavicular sac, or syringeal air sacs, and is directed cranially and ventrally towards the interbronchial region. (Pl. XXI., fig. 11.) The other subdivision passes ventrally, and expands into the large anterior thoracic air sac. (Pls. XXIII. and XXIV., figs. 17-24.) The stem of the syringeal air sacs, after emerging from the lung, passes up close to the ventro-medial region of the bronchus, and begins to expand into several large air sacs, which take up different positions, in relation to different parts of the syrinx. (Pls. XXI., XXIII. and XXIV., figs. 11, 17, 19.) There are three main sacs arising—a ventro-lateral interbronchial, and dorsal, which latter is the continuation of the stem.

The ventro-lateral one passes over the bronchus and ventral triangular plate, and takes up a position in relation to the whole ventro-lateral region of the syrinx and bronchus. (Pls. XXI. and XXII., figs. 11-14.)

On the right side the interbronchial sac passes up between the bronchi as far as the pessulus, and extends to the left bronchus, so as to form the inner boundary of both membranæ internæ.

On the left side the sac is much smaller, not reaching to the pessulus, and confined to its own side. (Pls. XXI. and XXII., figs. 11-13.)

The third main sac, or dorsal one, is large, and gives off three main divisions before terminating. (Pls. XXI., XXII., XXIII., figs. 11-16.) The most cranial one passes laterally behind the bronchus into a large expanded sac occupying the whole of the dorso-lateral region of the syrinx. Just caudally, the second smaller division also passes dorso-laterally, beneath the bronchus, to the lateral side. The third division is large, and passes laterally, giving off diverticula to the upper region of the lung. It passes dorsal to the bronchus, and in close relation to the innominate artery. This is the recurrent bronchial branch of the interclavicular sac. (Pl. XXIII., fig. 15.) After giving off its three main divisions, the main dorsal sac terminates in several small

diverticula in the lung region. In this way are formed the recurrent branches, large and small, of the interclavicular sac.

The ventro-lateral and dorso-lateral syringeal sacs press close against the *membranae externae, tracheales* and bronchus. They are also in close contact with each other, and overlie the dorsal and ventral triangular plates. Thus all surfaces of the syrx—dorsal, ventral, lateral and interbronchial—are embraced by air sacs.

8. Seventeen to twenty-one days.—The development of the syrx after the close of the sixteenth day is one of degree rather than the laying down of any new structures, hence the remaining days of incubation are taken together. There are a few changes in the supporting framework. There is first a histological change. The hyaline or cartilaginous matrix is gradually laid down, and the cartilaginous cells come to lie in their characteristic lacunae. On hatching, the left ventral end of the penultimate ring ceases to be fused with the ventral triangular plate, so that only the last ring is now fused to the plate. (Pl. XX., fig. 8.) Dorsally, the downturned ends of the fifth-last ring are bound to the apex of the plate by tissue, which becomes fibrous in the adult. A slight flattening has occurred in the rings embedded in the *membranae tracheales*, the intermediate ones being small, and bound together by a connective tissue. Hence the *membranae tracheales*, although thinner, are still far from being membranous. (Pl. XIX., fig. 2.) The *membranae internae* and *externae* have also become much thinner. The syringeal muscles are more strongly developed. There is now the dorsal and the ventral pair, but they do not extend further down the trachea than the twelfth or eleventh-last tracheal rings. The air sacs have now so completely surrounded the syrx as to separate it off from adjacent structures, such as the oesophagus and large vessels of the heart, which are in close relation to the tracheo-bronchial junction.

Other than the increased size of the elements of the syrx, this comprises the development up to the time of hatching.

V.—*Post-embryonic development.*

The syrx, being peculiar to birds as a vocal organ, shows considerable development in the post-embryonic period. This accounts for some marked differences between the adult and the hatched condition.

Since all the morphological structures of the syrx have been laid down during the embryonic period, the development in the post-embryonic period is chiefly histological, but to such a degree that

this tracheo-bronchial junction is converted into a truly membranous chamber, whose lateral walls are made up of the *membranae tracheales* and *externae*. The *membranae tracheales*, between the time of hatching and the adult condition, undergo much change. The last five tracheal rings embedded in it flatten into extremely thin band-like vestiges, while the tissue between them becomes thin and tough, so that the whole constitutes the stout *membranae tracheales* of the adult. The *membranae externae* become the most distinctive membranes, thin, yet strong, oval in outline, and stretched between the last tracheal ring and the well-marked first bronchial semi-ring.

A similar change occurs in the *membranae internae*. The bronchidemus gradually assumes the fibrous condition of the adult. As regards the supporting framework, the changes in the last five tracheal rings have been noted. The first two bronchial semi-rings become the most developed of all the syringeal rings, and they are curved so that their concavity looks cranially, and opposes that of the last tracheal ring. The dorsal and ventral plates considerably thicken and become very prominent, and only the ventral ends of the last tracheal ring fuse with it. Their basal angles, however, articulate with the other tracheal rings and first bronchial semi-rings.

In the older fowls, especially in the male bird, the pessulus becomes calcified, and may become partially ossified, not only along the whole extent of the rod, but also in the central portions of the dorsal and ventral triangular plates. In addition to this, there is a small centre of ossification in the ventral ends of the first bronchial semi-ring, just before it articulates with the basal angles of the ventral triangular plate. Ossification also takes place in many of the tracheal rings above the syrinx. The syringeal muscles change very little. There are the dorsal and ventral pairs, and they do not reach the syrinx. Finally, with the change in the external walls of the syrinx, the characteristic shape of the adult syrinx is assumed—namely, the lateral walls have approached one another, so that the lateral width of the syrinx is less than that of the trachea, but the dorso-ventral depth is somewhat greater.

As before, the whole syrinx is enveloped by the syringeal air sacs or diverticula of the interclavicular air sacs.

Summary.

In conclusion, the following points may be given as distinctive features of the syrinx of the common fowl:—

1. The formation of a syringeal chamber or "tympanum," with extensive membranous walls.
2. The presence of membranous internal bronchial walls, with the connecting bronchidesmus.
3. The presence of the bolt-like pessulus, with its ventral and dorsal triangular plates.
4. The very vestigial condition of the last five tracheal rings, the greater development of the first two bronchial semi-rings, and the close relationship of all these elements with the ventral and dorsal plates.
5. The very noticeable absence of muscles in direct or intimate association with the syringeal membranes.
6. The complex and intimate relationship of respiratory air sacs to the syrinx as a whole.

Literature.

Brunelli, G.—Riduz d. laringe sup e. svil d. siringe, etc. *Giornale ornitol. Ital.* Siena, 1904. (Not available to me for consultation.)

Garrod, A. O. H.—"On the conformation of the thoracic extremity of the trachea in the class Aves." Pt. I., Gallinae, *P.Z.S.*, 1879, pp. 354-380.

Hacker, V.—Ueber den unteren Kehlkopf der Singvögel. *Anat. Anz.*, 1898, pp., 521-532. *Gesang d. Vögel*, Jena, 1900.

Juillet, A.—Recherches Anatomiques, Embryologiques, Histologiques, et Comparatives sur le Poumon des Oiseaux. *Proceedings of Experimental and General Zoology*, Vol. 49, No. 3, Chap. IV., Jan., 1912.

Wunderlich, L.—Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des unteren Kehlkopfes der Vögel.

Nova Acta Acad. Caes. Leop. Carol. Germanicae, Bd. XLVIII., 1884.

DESCRIPTION OF PLATES XVIII-XXIV.

Figs. 1-3.—Median frontal or longitudinal horizontal sections through the tracheo-bronchial junction of the chick embryo at three stages, showing chiefly the elements of the cartilaginous framework, the developing membranes and the air sacs in relation to the syrinx.

- Fig. 1.—Stage of 13-14 days' incubation.
- Fig. 2.—Stage of 15 days' incubation; interbronchial air sacs in position, lateral sacs appearing.
- Fig. 3.—Stage of hatched condition; all the syringeal air sacs in position, and the whole structure rapidly approaching the adult condition.
- Figs. 4 to 10.—Frontal sections through the ventral and dorsal triangular plates of the pessulus at different stages, showing their relation to the tracheal rings, and the first bronchial semi-ring.
- Fig. 4.—Stage of 11-12 days' incubation, ventral triangular plate appearing, along with the four last tracheal rings, and first bronchial semi-ring.
- Fig. 5.—Stage of 13-14 days' incubation, ventral plate now well formed, with the four last rings fused to it. First bronchial semi-ring articulates, but is not fusing with the plate.
- Fig. 6.—Stage of 15 days' incubation. The ventral ends of the third-last tracheal ring are separated from the ventral plate. The second bronchial semi-ring is fused ventrally with the first bronchial semi-ring.
- Fig. 7.—Stage of 16 days' incubation. The right ventral ends of the second-last tracheal ring are now separated from the plate, as well as the ventral ends of the third.
- Fig. 8.—Stage of the hatched condition. The left ventral end of the third-last ring is separated from the plate, so that only the last tracheal ring has its ventral ends fused to the ventral plate.
- Fig. 9.—Stage of 13-14 days. Dorsal triangular plate appearing.
- Fig. 10.—Stage of 15 days. Dorsal plate well formed, with the various tracheal rings and first bronchial semi-ring articulating, but not fusing, with it.
- Figs. 11-16.—Stage of 16 days' incubation. Frontal, or longitudinal horizontal sections, through the region of the tracheo-bronchial junction, to show the arrangement and origin of the syringeal air sacs, derived from the interclavicular sac.
- Fig. 11.—The interclavicular sac is seen passing up from its common stem of origin with the anterior thoracic air sac into the interbronchial region, and opening ventrally at the cranial end of the bronchus, into the large ventro-lateral sac, situated behind the triangular plate, and lateral to the lower tracheal rings.

Fig. 1.

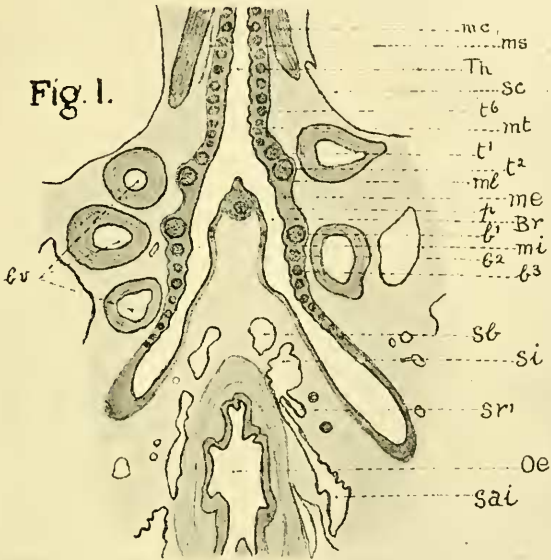


Fig. 2.

